



Diversity of native and alien plant species on rubbish dumps: effects of dump age, environmental factors and toxicity

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Abstract. The flora of 96 rubbish dumps consisting of organic, inorganic and industrial wastes was studied in the Czech Republic. Some dumps contained toxic substances (heavy metals, chloroethylenes, phenols, polychlorinated biphenyls, oil hydrocarbons and biogas). Statistically significant factors explaining the number and proportional representation of native plant species, archaeophytes (introduced before 1500) and neophytes (introduced later) were determined. In total, 588 species of vascular plants were recorded, with archaeophytes (133 species) over-represented and native species (322 species) and neophytes (133 species) under-represented compared to their proportions in the national flora. Minimum adequate models were used to determine the effects of several factors on species numbers and proportions, independent of other factors. Dump area, human density in the region and altitude (non-significant only in archaeophytes) were correlated positively with species numbers. Dump age, expressed as time since dump establishment, interacted with the dump toxicity; species numbers increased with dump age on non-toxic dumps, whereas on toxic dumps no increase in numbers was noted. For neophytes, dump toxicity also interacted with human density; the increase in numbers of neophytes with human density is more pronounced

on toxic than on non-toxic dumps. The variables measured failed to explain observed differences in proportional representation of native species, archaeophytes and neophytes. This suggests that the occurrence of species growing in such extreme habitats is driven overwhelmingly by factors such as anthropogenic disturbance. A possible explanation for the positive effect of altitude on species numbers on dumps is that the effect of heating of the deposited substrate by microbiological processes, documented by previous studies, overrides the effect of altitude which was shown repeatedly to have a negative effect on species richness. Neophyte distribution is driven by an interplay of factors distinct from those influencing the distribution of native species, namely toxicity and human density (the latter we interpret as a surrogate for propagule pressure). Their distribution on studied dumps is more restricted than that of native taxa and archaeophytes, and they are more limited by toxic substrata; more intensive propagule pressure is required for their establishment at dumps with higher toxicity levels.

Key words. Altitude, archaeophytes, biological invasions, Czech Republic, dump area, extreme substrata, neophytes, propagule pressure, species diversity, toxicity.

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INTRODUCTION

In Central Europe, human activity has resulted in the ongoing ruderalization of landscapes and creation of anthropogenic habitat types (Sukopp, 1969; Sukopp *et al.*, 1979; Kowarik, 1990).

Numerous studies have investigated the plant composition of human settlements at a variety of scales, so there is good knowledge of the factors promoting species richness and structuring vegetation composition in such sites (Sukopp *et al.*, 1990, 1995; Kowarik, 1995; Pyšek, 1998a,b; Wittig, 2002). Papers describing and analysing vegetation on human-made habitats in open landscapes are less common, and research on succession dominates such studies. So far, they have focused on large-scale spoil heaps from coal mining (Prach, 1987; Ninot *et al.*, 2001; Pyšek *et al.*, 2001; Wiegleb & Felinks, 2001), abandoned oldfields (Osbornová *et al.*, 1989) or disturbed sites associated with industry (Forbes & Jefferies, 1999). This research is of considerable practical importance (Prach *et al.*, 2001a; Pyšek *et al.*, 2001) and has contributed to the refinement of successional theory (Prach *et al.*, 2001b). Floristic papers describing floral composition on individual spoil heaps also exist (Rostanski, 1998).

Rubbish dumps composed of a mixture of organic and inorganic waste, established in the open landscape and used for waste accumulation for various periods of time, represent a habitat with variable geographical features, genesis and substrate toxicity (Sukopp, 1972; Kunick & Sukopp, 1975; Tauchnitz *et al.*, 1984; Pyšek & Hájek, 1996a,b). By providing suitable conditions for ruderal species, such places serve as foci for the further spread of agricultural weeds, alien plants and associated crop pests and pathogens to the surrounding landscape (Hudziok, 1967; Kunick & Sukopp, 1975; Slobodda, 1983). Previous studies of such habitats focused on restoration (Ettala, 1991) and succession (Kreh, 1935; Gutte, 1971; Kunick & Sukopp, 1975; Tauchnitz *et al.*, 1984; Pyšek & Hájek, 1996a), but no attempt has been made to use the extensive data sets to explain patterns of species diversity. Knowledge of factors determining species richness of such sites is not only of ecological interest (as any vegetation of such habitats provides challenging research opportunities to study plant responses to extreme conditions; Antonovics *et al.*, 1971; Bradshaw & McNeilly, 1981) but it is also of practical importance. The aims of this paper are to assess: (i) the relative importance of different factors in structuring plant species richness at rubbish dumps; (ii) the effect of toxic deposits on plant species richness; and (iii) whether plant

species diversity in these habitats is influenced by the same factors as in more natural habitats.

DATA

In 1995–97, the vegetation of 96 rubbish dumps in the Czech Republic (with the majority located in the western part of the country between 49°00' and 50°21' latitude, and 12°28'–16°57' longitude) was studied, the primary aim being to determine whether contaminating substances were leaking into the surroundings (Pyšek, 1983; Pyšek & Hájek, 1996a). Dumps comprised mixtures of municipal and industrial wastes including both organic (animal faeces, decomposing vegetable matter, paper, textiles and other solid wastes) and inorganic material (ashes, slag, building materials and other industrial wastes, including toxic chemicals; see Pyšek & Hájek, 1996a). Soil has been added occasionally to the deposited material. The volume of accumulated material ranges from 50 to 520 000 m³, the dump area is 10–50 400 m² (see Pyšek *et al.*, 2003 for exact location and size parameters of all localities studied). The presence of the following toxic substances was recorded: heavy metals (Al, As, Be, Fe, Mn, Zn), extremely high salt concentrations (Cl, SO₄, NO₂, NO₃, NH₄), di-, tri- and tetrachlorethylene, phenols, polychlorinated biphenyls, oil hydrocarbons and biogas; the 18 rubbish dumps contaminated by these substances were classified as 'toxic'. The period over which material has accumulated was termed 'dump age'. The surrounding landscape was classified into broad categories: arable land, meadows and grasslands, water courses, urban area and forest. Environmental factors were derived for each locality from existing Geographic Information Systems (GIS) layers; they include altitude, climate parameters related to precipitation and temperature and climatic districts (warm, moderate and cold), which are based on a combination of various climatic characteristics (Quitt, 1975). Human population density for each region was recorded as a surrogate for the intensity of disturbance and, in the case of alien species, also propagule pressure.

A complete list of vascular plants was recorded for each locality, and the species were divided into native and alien (following the terminology of Richardson *et al.*, 2000). The latter group was further divided into archaeophytes, introduced

to the Czech Republic before AD 1500, and neophytes introduced after that date (Holub & Jirásek, 1967; see Pyšek *et al.*, 2002c for historical information on alien species of the Czech flora). A complete lists of taxa recorded on the rubbish dumps studied was published in Pyšek *et al.* (2003). Nomenclature of plant species follows Rothmaler *et al.* (1982).

Statistical analysis

Data were evaluated using analysis of covariance (ANCOVA) in GLIM® version 4 (Francis *et al.*, 1994). The adequacy of the fitted models was confirmed by plotting standardized residuals against fitted values, and by normal probability plots of the fitted values (Crawley, 1993).

The response variables were the total numbers of species, the numbers of native species, archaeophytes and neophytes, and the relative proportions of native species, neophytes and archaeophytes of the total. Data on proportions were transformed into logits. The logit, $\ln(p/1-p)$, is a linearization technique that gives in GLIM® the link function relating the linear predictor, $b_0 + b_1x$, to the value of the response variable by the expression

$$\ln(p/1-p) = b_0 + b_1x.$$

In this expression, p is the proportion of the total number of species from which p has been drawn, x is the explanatory variable and b_0 and b_1 are the regression coefficients (Crawley, 1993: 267–8). To prevent the logits that were estimated from small samples having undue influence, logits were weighted by the total number of species in each rubbish dump. The errors in the response variables were assumed to be binomially distributed (Cox & Snell, 1990), and overdispersion of binomial errors treated by Williams' adjustment of unequal binomial denominators (Crawley, 1993: 351–353; Pyšek *et al.* 2002a). The data on the total numbers of species, native species, archaeophytes and neophytes were square root-transformed to obtain an appropriate for count data (e.g. Sokal & Rohlf, 1981: 421–423), and evaluated using normal errors and identity link function.

The explanatory variables were human density (with the categories being < 60, 60–100, 100–150 and > 500 inhabitants per km²), dump features and geographical characteristics. The dump features

included the habitats present in the surroundings (arable land, forest, meadows and grasslands, urban areas and water courses), and toxicity (yes, no) as factors, and the dump area (10–50 400 m²) age (4–73 years) and the number of surrounding habitats (1–4) as covariates. Geographical characteristics included altitude (290–855 m a.s.l.) and climate (expressed as climatic districts on an ordinal scale 3–12 increasing from cold to warm; Quitt, 1975); in the case of their significance ($P < 0.05$), they were replaced and further treated by the use of weather covariates: annual precipitation (450–500, 500–550, 550–600, 600–650, 650–700, 700–800, 800–900, 900–1000 mm), precipitation in the growing season (300–350, 350–400, 400–450, 450–500, 500–600 mm), mean annual temperature (5–6, 6–7, 7–8, 8–9 °C), January isotherm (–5 to –4, –4 to –3, –3 to –2, –2 to –1 °C) and June isotherm (12–13, 13–14, 14–15, 15–16, 16–17 °C). Because the proportions of archaeophytes and neophytes have been shown repeatedly to be affected consistently by the number of native species (Lonsdale, 1999; Pyšek *et al.*, 2002a), these data were analysed using the number of native species as a covariate. To achieve a comparable influence, all covariates were standardized to have a zero mean and variance of one.

The aim of each analysis was to determine the minimal adequate model. In this model, all explanatory variables (factors and covariates) were significantly ($P < 0.05$) different from zero and from one another, and all non-significant explanatory variables were removed. This was achieved by a stepwise process of model simplification, beginning with the maximal model (containing all factors, interactions and covariates that might be of interest), then proceeding by the elimination of non-significant terms (using deletion tests from the maximal model) and retention of significant terms. This evaluation was carried out using a newly developed approach (Pyšek *et al.*, 2002a,b), based on Lonsdale (1999). To prevent biases to the model structures caused by correlation between variables, model simplifications were made by backward elimination from the maximal models by using stepwise analysis of deviance tables (e.g. Crawley, 1993: 192–197). The results obtained were thus not affected by the order in which the explanatory variables were removed in the stepwise process of model simplification.

In the maximal model, the interactions were fitted by each covariate regressing on each factor with a different intercept and a different slope. In the first step of model simplification, the different slopes of each covariate on each factor were replaced in turn by a common slope of each factor on each covariate. The common slopes were

regressed on the factors one after another, and the changes in residual deviance caused by removal of the different slopes for each covariate were assessed. After all covariates with a common slope were assessed, all non-significantly different slopes were deleted, and a reduced model was assessed. The analysis then continued

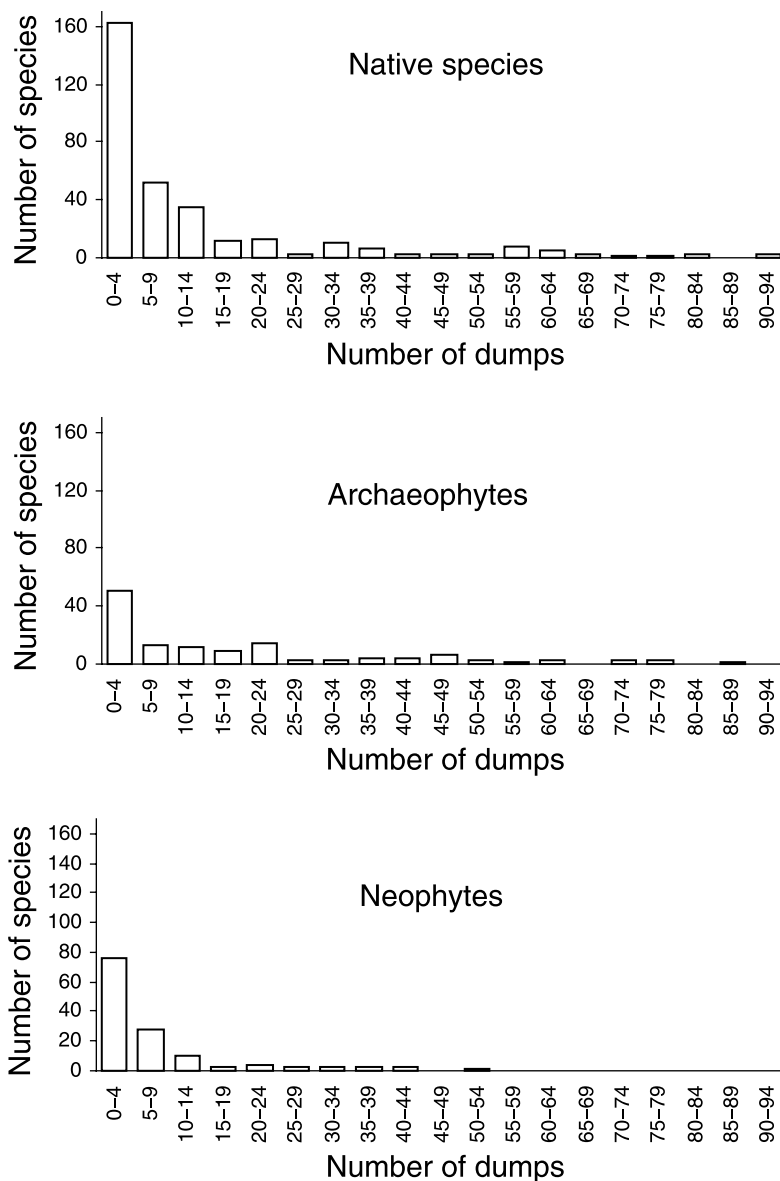


Fig. 1 Frequency distribution of the number of species in each origin grouping (native species, archaeophytes and neophytes) according to the number of dumps in which they were found.

on the reduced model. In this model, all the remaining terms were deleted in turn from the reduced deviance table, and only those leading to a significant increase in residual deviance were retained. The deletion tests were repeated on the reduced models until, after removal from the last deviance table, the minimal adequate model that contained nothing but significant terms was determined.

RESULTS

Structure of the flora on rubbish dumps

A total of 588 species of vascular plants were recorded on the rubbish dumps studied, representing 13.5% of the documented national flora (Kubát *et al.*, 2002; Pyšek *et al.*, 2002c). Of these, 322 species are native (54.8% of the total), 133 archaeophytes (22.6%) and 133 neophytes (22.6%). Comparing the overall frequencies on rubbish dumps with the overall frequencies in the flora of the Czech Republic, archaeophytes are over-represented on dumps (8.1% national representation), whereas native species and neophytes are under-represented (66.7 and 25.3%, in the national flora, respectively) (Pyšek *et al.*, 2002c). These overall differences in frequencies are highly significant (*G*-test on contingency tables, $\chi^2 = 95.63$; d.f. = 2; $P < 0.0001$).

Frequency distributions of the three groups show remarkably distinct patterns (Fig. 1). Among neophytes, 78.2% species do not occur on more than 10 dumps and only one species (*Trifolium hybridum*) was recorded on more than half the dumps (57.3%). On the other hand, 9.8% of native species and 7.4% of archaeophytes were found on more than 50% of dumps. Although the total numbers of archaeophytes and neophytes are the same, a very skewed distribution of neophytes results in a higher average number of archaeophytes per dump (33.0 ± 8.6) than that of neophytes (12.1 ± 5.8) (Wilcoxon's rank-sum test: normal statistic with correction $Z = 8.40$; $P < 0.0001$).

The following taxa are most represented, in terms of the number of rubbish dumps occupied, and occurred in at least 75% of localities: *Urtica dioica* (97.9% of the dumps), *Artemisia vulgaris* (97.9), *Agropyron repens* (86.5), *Rumex obtusifolius* (83.3), *Chenopodium album* (80.2), *Taraxacum*

sect. *Ruderalia* (77.1) among native species and *Cirsium arvense* (89.6), *Tripleurospermum inodorum* (82.3), *Plantago major* (81.3), *Atriplex patula* (75.0) and *Arctium tomentosum* (75.0) among archaeophytes.

Factors affecting the total number of species

The minimal adequate model for the total number of species explains 45.0% of the variance in species richness (Table 1). Dump area has the most important effect on species richness and explains 21.9%. Human density explains 9.7%, the interaction between dump age and toxicity 7.6%, and altitude 5.8% of variance in species richness (Table 1).

Increasing area and a high human density positively affected species richness (Fig. 2a,b). However, the effect of dump age on species richness was dependent on toxicity. Species richness increases with age on non-toxic dumps but decreases on toxic dumps (Fig. 3a). However, the overall decrease on toxic dumps was due largely to one, very old, dump. If we ignore this dump, the effect of age is no longer significant (deletion test: $F = 0.07$; d.f. = 1,90; NS). Species richness increases significantly on non-toxic dumps, and does not change on toxic dumps ($F = 5.13$; d.f. = 2,1; $P < 0.01$).

Increasing altitude also positively affects species richness (Fig. 2c). However, there is no significant effect of climate (deletion test: $F = 1.15$; d.f. = 1,83; NS). When the effect of altitude is replaced by the weather variables, the analysis does not indicate any significant effect of annual precipitation ($F = 1.52$; d.f. = 1,87; NS), precipitation in the growing season ($F = 1.21$; d.f. = 1,87; NS), mean annual temperature ($F = 0.016$; d.f. = 1,87; NS), January isotherm ($F = 2.27$; d.f. = 1,87; NS) and June isotherm ($F = 0.18$; d.f. = 1,87; NS).

No significant effect was detected for habitats in the surroundings ($F = 1.63$; d.f. = 4,86; NS), nor for their number ($F = 0.23$, d.f. = 1,83; NS).

Factors affecting numbers of native species, archaeophytes and neophytes

The minimal adequate models for particular species groups differ in the amount of variance explained (40.2% for native species; 23.6% for archaeophytes; 43.1% for neophytes). Area, human

Table 1 The minimal adequate model for the total number of species

Parameter	Estimate ¹	SE	Explained variance (%)	d.f.	F	P
Common intercept	8.801	0.161				
Area ²	1.041	0.167	21.9	1,91	38.97	< 0.000
Human density ²	0.695	0.167	9.7	1,91	17.26	< 0.000
(Age) × (no toxicity) ²	0.989	0.316	7.6	2,92	6.74	< 0.01
(Age) × (toxicity) ²	-0.357	0.190				
Altitude ²	0.54	0.168	5.8	1,91	10.31	< 0.01
Total			45.0	5,90	17.52	< 0.000

¹ Square root of numbers. ² Slope.

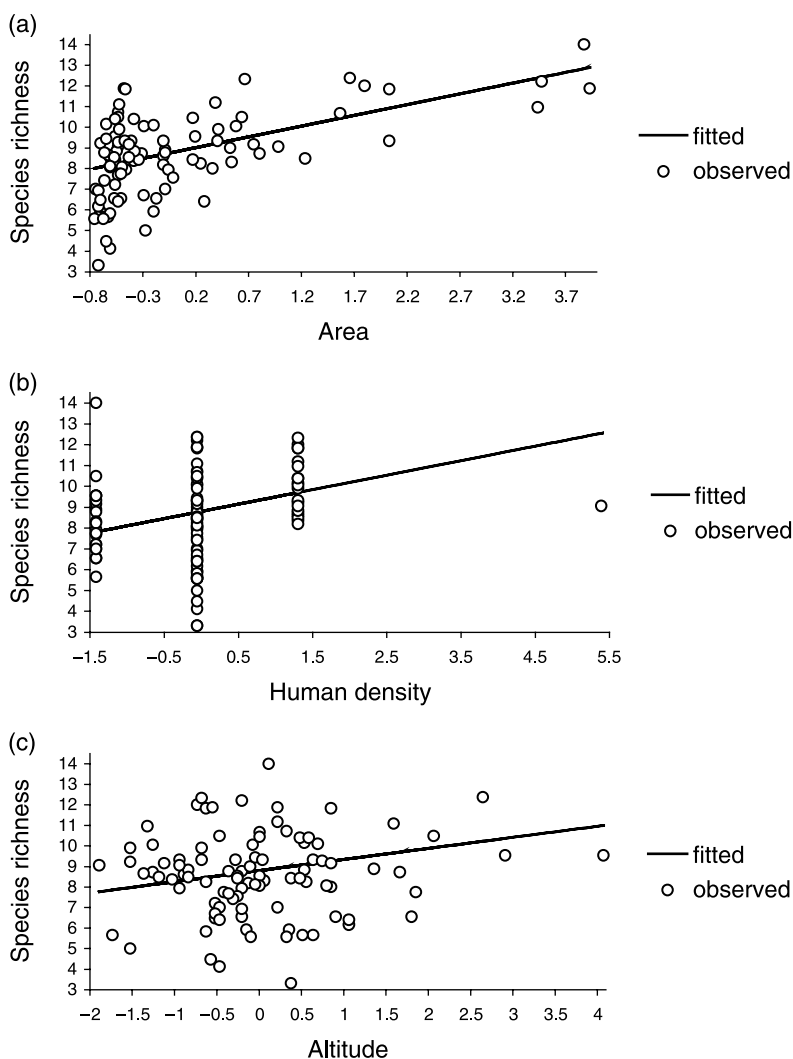


Fig. 2 Observed and fitted values for the standardized explanatory variables positively influencing the total number of species. (a) Area; (b) human density; (c) altitude. Species richness is expressed as the square root of the total number of species. Parameters of the fitted values are given in Table 1.

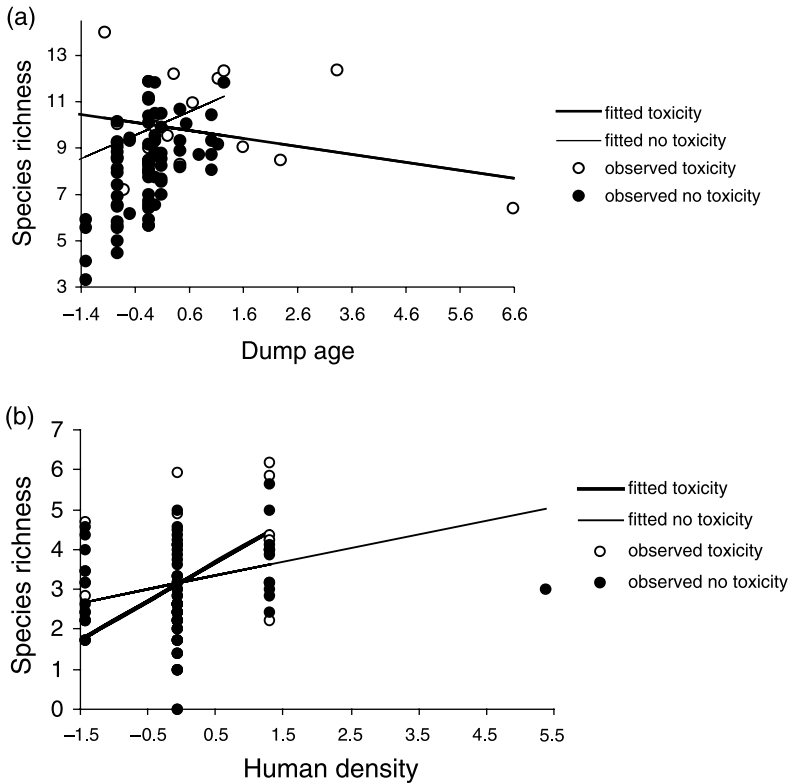


Fig. 3 Observed and fitted values of species richness (square root of species numbers) in interactions including toxicity. (a) Toxicity and standardized dump age for the total number of species; (b) toxicity and standardized human density for neophytes. Parameters of the fitted values are given in Tables 1 and 4.

Table 2 The minimal adequate model for native species

Parameter	Estimate ¹	SE	Explained variance (%)	d.f.	<i>F</i>	<i>P</i>
Common intercept	6.355	0.115				
Area ²	0.793	0.119	25.3	1,92	44.46	< 0.000
Human density ²	0.315	0.120	3.9	1,92	6.95	< 0.01
(Age) × (no toxicity) ²	0.520	0.229	2.4	1,93	4.24	< 0.05
(Age) × (toxicity) ²	NS					
Altitude ²	0.463	0.119	8.6	1,92	15.05	< 0.000
Total			40.2	4,91	21.16	< 0.000

¹ Square root of numbers. ² Slope.

density and altitude (with the exception of archaeophytes) are always significant and positively correlated with species richness. The interaction between dump age and toxicity always has a significant effect. For native species, the importance

and explanatory power of particular variables follows the same general pattern as described for the total number of species, with one exception: species richness on toxic dumps did not decrease with dump age (Table 2). This deviation from the

Table 3 The minimal adequate model for archaeophytes

Parameter	Estimate ¹	SE	Explained variance (%)	d.f.	F	P
Common intercept	5.015	0.121				
Area ²	0.425	0.119	8.7	1,93	11.53	< 0.01
Human density ²	0.408	0.116	9.4	1,93	12.47	< 0.001
(Age) × (no toxicity) ²	0.656	0.241	5.5	1,93	7.39	< 0.01
(Age) × (toxicity) ²	NS					
Altitude ²	NS					
Total			23.6	3,92	13.67	< 0.000

¹ Square root of numbers. ² Slope.

Table 4 The minimal adequate model for neophytes

Parameter	Estimate ¹	SE	Explained variance (%)	d.f.	F	P
Common intercept	3.137	0.106				
Area ²	0.471	0.110	11.9	1,90	18.31	< 0.000
(Human density) × (no toxicity) ²	0.366	0.119	14.7	2,91	11.28	< 0.000
(Human density) × (toxicity) ²	0.917	0.233				
(Age) × (no toxicity) ²	0.653	0.208	19.6	2,91	7.36	< 0.01
(Age) × (toxicity) ²	-0.276	0.128				
Altitude ²	0.366	0.112	6.9	1,90	10.64	< 0.01
Total			43.1	6,89	10.76	< 0.000

¹ Square root of numbers. ² Slope.

general species richness model was also true for archaeophytes. As noted above, archaeophytes were the only group for which altitude was not a significant factor, and human density is as important as dump area and explains slightly more variance (9.4 vs. 8.7%, Table 3).

In neophytes, human density interacts significantly with dump toxicity; this interaction explains 14.7% and is the most important predictor (Table 4). Increase in the number of neophytes with human density is more pronounced on toxic than on non-toxic dumps (Fig. 3b). However, as in the case of interaction between dump age and toxicity, this interaction is driven largely by a single data point (this time by a single toxic site with the highest human density located in Prague). After deleting this site, the interaction between density and toxicity is only marginally significant ($F = 3.17$; d.f. = 1,89; $P = 0.08$). As for native species and archaeophytes, the model then indicates a highly

significant positive effect of human density on species richness, independent of dump toxicity ($F = 18.92$; d.f. = 1,90; $P < 0.000$; $R^2 = 12.7\%$). Similarly, the significant interaction between dump age and toxicity, causing significant decrease on toxic dumps (Table 4), is only significant, as for the total number of species (Table 1), if the single very old toxic dump is included (deletion test: $F = 0.0009$; d.f. = 1,89; NS). After its removal, species richness increases significantly on non-toxic dumps, and does not change on toxic dumps.

Particular weather variables and surrounding habitats do not affect species numbers significantly in any of the analyses. Similarly, human density, dump characteristics and geographical parameters have no significant effect on the proportional representation of native species ($\chi^2 = 48.18$; d.f. = 46; NS), archaeophytes ($\chi^2 = 54.76$; d.f. = 52; NS) and neophytes ($\chi^2 = 49.72$; d.f. = 52; NS).

DISCUSSION

Rubbish dumps are a distinct habitat in the Central-European landscape. They are considered as potential foci for the further spread of agricultural and environmental weeds and other noxious biota to the surroundings (Hudziok, 1967; Kunick & Sukopp, 1975; Slobodda, 1983). Such habitats represent important sites not only for plants, but perhaps even more for other groups of non-native organisms. Odegaard & Tommeras (2000) reported that compost heaps in northern Europe function as a refuge for 34 alien beetle species, 12 of which have established in natural habitats. No comparable analyses have been made for plants, but there is evidence that rubbish dumps of specific kinds can contribute to the spread of alien flora, for example from wool-processing wastes used as fertilizer (Dvořák & Kühn, 1966).

Compensated effect of altitude?

Rubbish dumps possess unique environmental features unparalleled in natural but also in other human-made sites. Of these, temperature regime and toxicity are most distinct. Remarkably high substrate temperatures, compared to natural substrata, have been documented and are probably generally valid for refuse dumps (Kunick & Sukopp, 1975). In the initial stages of dumps composed of communal wastes from houses, temperature can reach 88 °C (Pierau, 1968). In a 2-year-old-rubbish tip, temperatures at 30–40 cm depth were on average 15–25 °C, with local maxima of 45 °C (Neumann, 1971). Although substrate temperature was not measured in our study, the character of studied dumps did not differ from those reported in the literature (Neumann, 1971; Kunick & Sukopp, 1975). We therefore believe that this phenomenon might be a clue to the surprising relationship between species richness and altitude, which was positive for natives and neophytes. This contradicts a negative relationship between number of species and altitude, which is common in the temperate zone and holds across a wide range of habitat and vegetation types (Rahbek, 1995; Pyšek *et al.*, 2002b). Low temperature at higher altitudes is the main determinant of increasing environmental harshness. This effect could be compensated by heating processes in the body of the dump and make it relatively

independent of the surrounding conditions. However, why the relationship is positive (with the exception of archaeophytes) is unclear; it should be pointed out that the analytical approach adopted in the present paper ensures that it is not an artefact of data structure. The variance explained by altitude ranges between 5.5 and 8.6% which, given the character of the data and variance usually explained by such studies (e.g. Lonsdale, 1999; Pyšek *et al.*, 2002a,b) suggests that this factor should not be disregarded as unimportant, and the effect of substrate heating on species richness on dumps deserves further study.

Effect of toxicity: different impact on different plant groups

Rubbish dumps are highly variable in terms of composition. Some wastes are relatively benign, comprising mainly cinders, concrete, steel smelter slag, pulverized fuel ash and various forms of lime, whereas others are highly toxic, comprising for example chromate waste, spent iron oxide and heavy metal residuals. Strongly alkaline reactions have been reported from toxic dump sites, with pH values of up to 12.7 (Gilbert, 1989). Tauchnitz *et al.* (1984) showed on a set of German toxic rubbish dumps that, depending on the type of dump and material accumulated, C/N values varied enormously between 16 and 100, pH from 1 to 12, salt content from 0.05 to 3.28%, *K*-value 11–175 mg/100 g, and P contents between 0.2 and 17.3 mg/100 g. These values illustrate that extreme chemical variability of the substratum could play an important role in shaping the plant composition of rubbish tips. The same study reported that pH values lower than 6 and exceeding 8 lead to a slower vegetation succession (Tauchnitz *et al.*, 1984). In another study of the vegetation on dumps, Kunick & Sukopp (1975) reported elevated Cd and Cu levels, with high toxic values being common.

There is evidence that high concentrations of toxins may be responsible for the absence of sensitive plant species; the tolerance of particular plant species varies considerably (Antonovics *et al.*, 1971; Ernst, 1974; Banášová & Hajdúk, 1977; Snowden & Wheeler, 1993). The present study indicates that toxicity is likely to have an effect on species richness, and that the relationship is

not trivial. The following conclusions can be drawn from the results.

It appears that the older the dump, the more species it harbours. This effect is unbiased by the methodological approach because all dumps were in active use when sampled. The gradual enrichment is associated with successional processes (Prach *et al.*, 2001a) because material, some of which carries propagules, is being deposited in a distinct manner (starting at the dump margin and gradually filling in to the opposite side) and as the accumulation proceeds, it creates a mosaic of successional stages. These stages harbour different species, and increase the overall species diversity on a dump. This pattern is valid regardless of dump size.

The significant relationship between dump age and toxicity, however, is consistent with the hypothesis that once toxic substances are deposited their gradual accumulation eliminates certain species and total diversity does not increase. However, this pattern varies depending on each plant group's origin. All groups are negatively affected by dump toxicity, as there is no increase in numbers for any group with increasing dump age on toxic dumps. However, neophytes (Pyšek *et al.*, 2002c) seem to be the most vulnerable group as their number decreased most with toxic substrata accumulated over time.

It should be noted that significance of some of the interactions revealed in the present paper depends on single dumps with rather distinct features, i.e. one very old toxic site and one located in the region of an extremely high population density. Nevertheless, even when these data points are ignored, the conclusions about the differences between the toxic and nontoxic (in the case of total species richness) and more and less populated areas (in the case of neophytes) are still valid. This shows that species numbers on toxic dumps do not increase as they do on non-toxic localities. Moreover, considering the sites with unparalleled features is justified here because it has a biological meaning; a long-term accumulation of toxic wastes is an important ecological effect. For data sets such as this, which cannot be manipulated experimentally and where it is impossible to add more sites to the analysis to prove the pattern, it seems better to take all sites into account and to be aware of their character when interpreting the results.

Human density as a surrogate of propagule pressure

Although the relationship between regional population density and site-specific disturbance is not necessarily strong, previous studies have shown that population density is an important determinant of distribution of particular species (Pyšek *et al.*, 1998) and of the pattern of flora richness in both disturbed (Pyšek, 1998a) and natural habitats (Pyšek *et al.*, 2002a). In the present study, human density is more a surrogate for propagule pressure for alien species than a surrogate for disturbance intensity because all rubbish dumps are heavily disturbed. Neophytes are most affected by this factor. Unlike native species and archaeophytes, they are probably less likely to be present in the landscape in the form of a seed bank and rely more on external input of propagules. This is associated with the fact that: (i) many native species on dumps are omnipresent weeds of arable land as are the majority of archaeophytes (Pyšek, 2001), hence forming extensive seed banks; and also that (ii) recent newcomers to the flora have restricted distributions compared to native species (Crawley *et al.*, 1996). In the present study, this is supported by the frequency distribution of numbers of dumps occupied by particular species (Fig. 1); the majority of neophytes are rare.

The importance of propagule pressure can be further inferred from the joint effect of human density and toxicity on the number of neophytes. The two factors interact but, unlike dump age, human density has a positive effect on both nontoxic and toxic dumps (Fig. 3b). For neophytes, the input of propagules can be considered as dominating factor underlying their presence on rubbish dumps. The results indicate that negative effects of toxicity might be compensated for as the increase in the number of neophytes with human density was more pronounced in toxic than in non-toxic dumps. Although the statistical significance of this finding is driven by a single non-toxic dump outlier, we believe that this finding has a biological meaning. Moreover, even if the outlier is ignored, the result is still marginally significant ($P = 0.08$), indicating a rather robust statistical pattern. It seems that in toxic dumps, more propagule pressure is needed and this may be why the species richness of neophytes

is more closely dependent on human population density.

Dumps are extremely disturbed habitats; the occurrence of species they harbour is overwhelmingly driven by anthropogenic factors, rather than the range of ecological factors that shape the composition of flora in less extreme habitats (e.g. Bruun, 2000; Kessler *et al.*, 2001; Pyšek *et al.*, 2002a). This also holds for native species on dumps; they are not a random selection from the entire native Czech flora, but rather a subset of species common to urban landscapes (Sukopp *et al.*, 1979). Central-European terminology refers to these species as 'apophytes', defined as native species growing in human-made habitats, some of which no longer have their original habitats in the current landscape (Holub & Jirásek, 1967). In general, this makes this subgroup of natives more similar, in terms of biological and ecological features, to naturalized or invasive alien plants (Richardson *et al.*, 2000), especially neophytes, as these are generally transported by humans from anthropogenic landscapes. As a result, the proportional representation of the three groups on dumps in the Czech Republic seems to be unpredictable using the factors taken into account in the present study. However, the same factors were shown to describe well the proportional representation of these groups in nature reserves (Pyšek *et al.*, 2002a), in which the gradients of ecological factors shaping species distributions were wider.

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